GRASSES AND THE CULTURE HISTORY OF MAN

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ABSTRACT

The beginnings of plant and animal husbandry are lost in antiquity. It is not possible to determine from the available archaeological record when plant domestication was initiated. Changes in phenotype, however, known to be associated with cereal species under domestication, and preserved in the archaeological record indicate that growing crops was an established way of life some 10,000 years ago. There are four major domesticated cereal complexes. Three evolved in the Old World and one in the New World. Wheat, barley, rye and oats are Near Eastern cereals, and spread across Eurasia early during the history of agriculture. Rice is the principal cereal of South Asia, sorghum and pearl millet the major cereals of the African savanna, and maize is a domesticate of Mesoamerica. Why the shift from hunter-gatherer to settled agriculturist occurred during the culture history of man is not known. Food production may have been initiated when man was faced with a gradual reduction in productivity of effort required to maintain accepted standards of living, traditional group size, and social organization. Once initiated, population pressures in particular will tend to demand agriculture. Hunter-gatherers live in equilibrium with the environment and have little lasting effects on nature. Farming, by its very nature, destroys the natural environment. Habitats are permanently altered, and a return to hunting and food gathering becomes impossible. Survival of civilized man has become absolutely dependent on cereal agriculture. Overpopulation, depletion of resources, planetary pollution, and the social ills of cities are penalties we have to pay for the pleasures of an abundant and stable food supply.

Grasses have been playing a principal role in shaping the culture history of man every since he became sapient. They are basic to human life. The staple food of the great majority of mankind comes from grasses and they provide food for the grazing animals from which man derives most of his protein. The Gramineae is a relatively young but successful family. It includes an estimated 600 genera and 8,000 species that are widely distributed across the world. Grasses occur on all continents, including Antarctica, and are absent only from regions that are too barren or too cold to support the growth of flowering plants. The fossil record of grasses is meager, but there is good evidence to suggest that they emerged as a distinct family during late Cretaceous times when the flowering plants were spreading throughout the world. By early Miocene grasslands probably were assuming a prominent place in the earth's vegetation, and it is estimated that at present almost one-quarter of the world's plant cover is composed of grass (Barnard, 1969). The evolution of the family has been strongly influenced by herbivorous mammals. Early ungulates were probably browsing, rather than grazing animals. Nonruminant kinds of Artiodactyla appear in the fossil record from the early Tertiary. Ruminant forms, particularly the Bovinae, arose during the Miocene and have coevolved with grasses ever since. The transverse intercalary growth zone in leaves and above culm nodes, the short internodes of aerial stems of annual grasses, and the tufted habit of perennial grasses during vegetative growth, are adaptations to withstand grazing.

Man appeared on the scene well after the Gramineae and grazing ungulates became widely dispersed. Hominid evolution dates back to the Pliocene, but the

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genus *Homo* appears in the fossil record only since the Pleistocene, and our own species is probably less than 100,000 years old (Isaac & Leakey, 1979). Man started as a hunter and gatherer of plants for food. He competed with animals for the available supply of plant food, and hunted some of these same animals to satisfy his craving for meat. Gradually man learned how to control the food resources in the areas where he lived. Selected animals were protected from their natural enemies, and populations of favored food plants were increased through planting. Plant and animal domestications were initiated, and man started on a path of rapid social evolution.

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THE DOMESTICATION PROCESS

The beginnings of domestication are lost in antiquity. It is not possible to determine from the available archaeological record when plant or animal husbandry was first practiced. But, changes in phenotype, known to be associated with particular plant and animal species under domestication and preserved in the archaeological record, indicate that growing crops and herding animals were established ways of life some 10,000 years ago (Higgs, 1972).

The transition from hunting-gathering to plant and animal husbandry occurred in different ways in different parts of the world. Different plant and animal species were domesticated at different times and places across the range of their intensive exploitation by man. Full pastoral nomadism is practiced only in the Old World, and only in areas where growing crops is impossible or totally unreliable as a constant source of food. In the wet tropics and high Andes of South America where grasses are not abundant, cultivation of tubers made settled agriculture possible. On the plains of Africa and Eurasia, and on the highlands of Mesoamerica, grass cultivation provided the staple food for a sedentary way of life. Domesticated plants depend on man for suitable habitats. This dependence on man-disturbed habitats came about through selection pressures associated with harvesting and sowing (deWet & Harlan, 1975). Weeds are similarly adapted to permanently man-disturbed habitats. The major difference is that weeds are usually spontaneous in this habitat while domesticated taxa depend on man for propagation. The ecological boundaries between the wild, weed and domesticated classes of plants are poorly defined. Wild plants may be aggressive natural colonizers and they are consequently weedy. Weeds may be protected, and wild plants may be cultivated as sources of food. Animal fonio, Brachiaria deflexa (Schumach.) C. E. Hubbard is collected in West Africa as a wild cereal. On the Fouta-Djalon highlands of Guinea it is a cultivated cereal (Portères, 1951), and in Angola the species aggressively invades cultivated fields where it is often protected and harvested as a crop (deWet, 1977). Domesticated species may behave as weeds when they have not completely lost the ability of natural seed dispersal. True fonio, Digitaria exilis (Kippist) Stapf is widely cultivated in West Africa (Portères, 1955). Its wild progenitor is not not known. But, the cultigen commonly escapes and occurs as a weed in the fields of other crops, where it is often harvested.

Cultivated cereal species are annuals, and their closest wild relatives are aggressive annual colonizers of disturbed habitats. The only exception is *Bromus mango* Desv. (mango). This biannual was cultivated in Chiloé province of central

Chile, until the eighteenth century, when it was replaced by the introduced Old World cereals wheat and barley (Gay, 1865; Molina, 1782; Cruz, 1972). Today *B. mango* is known only as a wild plant, distributed in Central Chile and adjacent Argentina (Parodi & Hernández, 1964).

Colonizing ability is essential in domestication. Propagation by man of selected genotypes, however, constitutes domestication. Sowing of seeds harvested from a planted population results in loss of seed dormancy, an increase in seedling vigor, and eventually the inability of the cultigen to successfully invade natural habitats (deWet, 1975, 1979). Phenotypic traits associated with sowing of annual seed crops are uniform population maturity, and commonly also an increase in fruit size. Harvesting in association with sowing leads to a reduction in natural seed dispersal ability, and uniform individual plant maturity (Harlan et al., 1973). Phenotypic characteristics associated with harvesting are usually persistence of spikelets or florets on the inflorescence after maturity, and either reduction of inflorescence-bearing culms or synchronized tillering. Fully domesticated cereal species depend on man for a suitable habitat as well as seed dispersal. The domestication process continues as long as the cereal is harvested and sown in successive generations. Selection pressures associated with harvesting and sowing are commonly superimposed on pressures induced by man in selecting for traits to satisfy his fancies. This leads to rapid evolution under domestication. Genetic drift, selection, and isolation allow for phenotypically different kinds of a domesticated species to be grown by different groups of people for the same or different uses. Cultivated grain sorghum, Sorghum bicolor (L.) Moench, as an example, is widely grown in Africa and Asia, morphologically variable, and frequently classified into 28 species with 165 botanical varieties and several hundred recognized phenotypes (Snowden, 1936). Genetically, these taxa are conspecific and represent little more than selections that are being maintained by man to suit his fancies and needs (deWet, 1978). Phenotypic changes associated with cereal domestication are often grotesque. The spike of wild pearl millet, Pennisetum americanum (L.) Leeke is at most 10 cm long (Brunken, 1977), while some cultivars have spikes over one meter long (Brunken et al., 1977). Even more spectacular are the differences that distinguish maize (Zea mays L.) from its closest wild relative Z. mays subsp. mexicana (Schrad.) Iltis (teosinte). Maize and teosinte are genetically conspecific, and evidence presented by Beadle (1977) suggests that teosinte is wild maize. These two taxa differ conspicuously from one another in four basic characteristics of the female inflorescence. First, the inflorescence is distichous in teosinte and polystichous in maize. Second, female spikelets are solitary at a rachis node in teosinte and paired in maize. Third, female spikelets of teosinte are individually sunken into indurated cavities on the rachis, each of which is closed by an indurated outer glume to form a fruitcase. In maize the paired spikelets are located in shallow, more or less indurated cupules. Fourth, fruitcases disarticulate at maturity in teosinte but cupules are persistent in maize. These opposing traits are not simple genetic alternatives (Galinat, 1975). Intermediate expressions of tunicate alleles determine induration, recessive alleles of a complex genetic system restores fertility to the rudimentary spikelet of a female pair, and recessive alleles of at least two

genes change the distichous spike of teosinte into the polystichous ear of maize (deWet, 1979).

Phenotypic changes associated with domestication are those selectively favored by man. The three principal innovations of cereal domestication, loss of natural seed dispersal ability, uniform population maturity, and uniform individual plant maturity facilitate harvesting, and increase the percentage of harvestable seed. Phenotypic changes characteristic of individual cereal species under domestication further increase yield, enhance threshing, or are designed to suit the fancies of the cultivator. Increase in inflorescence size commonly accompanies a shift from wild to domesticated. Cultivated maize from the Coxcatlán culture phase in the Tehuacán Valley of Mexico had less than 100 kernels per ear. Less than two millennia later kernel number had increased to over 600 per ear.

DOMESTICATED CEREALS

The principal use of grass by man is as cereals. Grasses are also highly valued as feed for livestock, and serve man in many other ways. Landscaping the habitat we live and play in is hardly complete without a lawn. There are turf grasses selected for house lawns, golf courses, parks, and sport fields. Grasses are also planted as ornamentals. No tropical garden is complete without a clump of bamboo, and Cortaderia selloana (Schult.) Ashers. & Graebn. (pampas) and Miscanthus sinensis Anderss. (eulalia) are popular lawn ornamentals in warm and temperate regions. Grasses provide us with food other than cereal grains. Sugar is extracted from the stems of domesticated Saccharum officinarum L. (sugar cane). In the Far East Zizania latifolia Turcz. (water rice) is grown as a vegetable. Fungus infests the lower leafbases and the swollen stems are eaten. The young shoots of Setaria palmifolia (Koen.) Stapf (jungle rice) are eaten in New Guinea, and the well-known bamboo shoots of commerce are harvested from species of Bambusa, Dendrocalamus, and Phyllostachys. Grasses are also used as fuel, timber, roofing material, and as material from which paper, mats, and containers are made. Two species, Cymbopogon citratus (DC. ex Nees) Stapf (lemon grass) and Vetiveria zizanioides (L.) Nash (vetiver), are commercially grown for their essential oils that are used in the perfume and pharmaceutical industries. Grasses serve man in many ways. But, it is their use as cereals that help shape his culture history. The caryopses of most grasses are edible, and at least 300 species are known to be harvested in the wild as cereals. Among these, 35 species belonging to 20 genera are, or were at one time grown as cereals (deWet, 1979). Brittle grass, Setaria geniculata (Lam.) Beauv., is known as a cultivated cereal only in an archaeological context from Mexico (Callen, 1965, 1967). Canary grass, Phalaris canariensis L., is grown as a food for caged birds rather than as food for man. American wild rice, Zizania aquatica L., has been harvested commercially in the wild for centuries, but it is only during the last decade that this cereal has been successfully cultivated (deWet & Oelke, 1978). Ethiopian oats, Avena abyssinica Hochst., is not consciously sown but is accidentally planted and harvested with other cereals. It is an obligate weed that has lost the ability of natural seed dispersal (Rajhathy & Thomas, 1974). The biannual Bromus mango (mango) was cultivated in central Chile until the eighteenth century, when it was replaced

by wheat and barley. The remaining 30 cereal species are still cultivated, although several of them as minor crops. The major cereals are wheat (*Triticum* spp.), rice (*Oryza sativa* L.), maize (*Zea mays*), sorghum (*Sorghum bicolor*), and pearl millet (*Pennisetum americanum*) in order of their importance as human food. It is estimated that in 1976 some 413 metric tons of wheat, 344 metric tons of rice, and 335 metric tons of maize were produced by the world's cereal farmers.

There are four major domesticated cereal complexes, each with a distinct geographic region of origin (Harlan, 1976). Three complexes evolved in the Old World and one in the New World. The small grains developed in the Near East, with wheat eventually becoming dominant across Eurasia, except for South Asia where rice is the principal cereal. The African savanna provided the world with sorghum and pearl millet, and maize is a domesticate of the highlands of Mesoamerica. The archaeological record suggests that southwestern Asia is the oldest region of cereal domestication, and that the knowledge of agriculture may have spread from here across the Old World and eventually to the New World (Carter, 1977). It is doubtful, however, that cereal agriculture evolved only once. Near Eastern cereals did become widespread across temperate Eurasia and Mediterranean Africa soon after they became domesticated. But, there is no evidence to suggest that the cereal complexes in South Asia, the African savanna, or Mesoamerica were not independently domesticated.

NEAR EASTERN COMPLEX

Three species of wheat, Triticum monococcum L. (einkorn), T. turgidum L.

(emmer) and $T. \times aestivum$ L. (bread wheat), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.) and rye (*Secale cereale* L.) are Near Eastern cereal domesticates. The Natufian of Palestine is the first known culture in the Near East that was equipped to extensively harvest and process small grains (Redman, 1977). Common tools used by the Natufian include grinding stones, stone mortars, and sickles with sheen on their stone blades. Extensive harvesting of cereals demand some kind of sickle, and since the florets of wild wheats and barley are tightly enclosed by glumes, processing is necessary to thresh the grain free.

Remains of wild barley and wild einkorn appear in the archaeological record at Tell Mureybit (Syria) dating back to between 10,050 and 9542 B.P. (Renfrew, 1969). This probably is the period of initial cereal cultivation in the Near East. Loss of natural seed dispersal ability is commonly accepted as indicating domestication of cereals in an archaeological context. However, cereals may have been cultivated for many generations before this domesticated phenotype became established. Domesticated wheat and barley, totally dependent on man for seed dispersal, appear in the archaeological records between 9500 and 8500 B.P. from numerous occupation sites (Harlan, 1977) extending from Turkey to southwestern Syria and Palestine. The practice of growing wheat and barley reached Greece by 8000 B.P., and during the next 2,000 years spread along the valleys of the Danube and Rhine to the Netherlands, and along the Mediterranean to France. Bread wheat, a strictly domesticated taxon, appears around 8000 B.P. in such scattered settlements as Knossos in Greece, Hacilar and Çatal Hüyük in Turkey, Tel Ramad in Palestine, and Tepe Sabz in Iraq (Renfrew, 1973). Domesticated oats and rye are rare or absent among archaeological plant

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remains dating back more than 7,000 years, although wild oats in particular seems to have been commonly harvested for at least 1,000 years before the species became domesticated. Harlan (1977) suggests that these two cereals were added to the Near Eastern complex as secondary crops. They invaded cultivated fields as weeds, were harvested, and eventually became domesticated. Rye is wild in Anatolia and Transcaucasia, and Evans (1976) proposes that the weed race evolved after the spread of cereal cultivation into these regions. When or where rye was first cultivated is not known. Oat is wild in the Mediterranean Basin and widespread in the Near East (Baum, 1977). Cultivated oat is reported from Greece by the late eighth millennium B.P., but the crop only became important some five millennia later and then in Central Europe (Holden, 1976). There is no evidence for an incipient food production period in Europe before the introduction of domesticated Near Eastern cereals (Waterbolk, 1968). Lakedwelling settlements such as at Niederwil in northeastern Switzerland, dating back to around 3700–3625 B.C., are characterized by fully domesticated barley and bread wheat, and *Chenopodium album* L., a species probably harvested in the wild as a pseudocereal (vanZeist & Casparie, 1974). Two other cereals, Panicum miliaceum L. (proso millet) and Setaria italica (L.) Beauv. (foxtail millet) occur in Swiss Lake Dwelling sites (Neuweiler, 1946). Wild foxtail millet occurs across Eurasia, but wild proso millet is known only from Central Asia (deWet et al., 1979; Kitagawa, 1979). It is possible that foxtail millet was independently domesticated in Europe and the Far East, but it seems likely that *Panicum* was introduced to Europe as a domesticated cereal (Werth, 1937). A single cereal, Avena strigosa Schrebn. (sand oats) is a truly European domesticate. Wild sand oats occurs in the western Mediterranean region and was probably domesticated as a secondary crop in Iberia. By the end of the prehistoric period, settled farming based on plant and animal husbandry, was an established way of life in Europe (Waterbolk, 1968). The spread of wheat and barley east into the Indus valley and into China was later than west into Europe. They became important cereals during the Harappa-Mohenjo Daro period between 2500 and 1700 B.C. (Vishnu-Mittre, 1968; Allchin, 1969), and along the lower Indus Valley at Chirand between 2500 and 1800 B.C. (Vishnu-Mittre, 1974). These cereals did not reach China until about 3500 B.P. (Ho, 1969).

Cereals were not the only field crops domesticated in the Near East. Almost as important as cereals are peas, *Pisum sativum* L. (Waines, 1975), broad beans, *Vicia faba* L. (Landizinsky, 1975; Zohary, 1977) and lentils, *Lens culinaris* L. (Ladinzinsky, 1979). These pulses appear in the archaeological record of the Near East as early as cereals. They spread with the cereals across temperate Eurasia, and together made possible the early civilizations of Mesopotamia, Egypt, Greece, Rome, and Europe.

ASIAN COMPLEX

Rice, Oryza sativa L., is the principal cereal of South and East Asia. Minor cereals belonging to the Asian complex are Coix lacryma-jobi L. (jobs tears) and Digitaria cruciata (Nees) A. Camus (raishan) from Assam, Echinochloa colona (L.) Link (shama), Brachiaria ramosa (L.) Stapf (anda horra) and Panicum su-

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matrense Roth. ex Roem. & Schult. (sawan) from South India, Paspalum scrobiculatum L. (khodo millet) and Setaria glauca (L.) Beauv. (korali) from Central India, Echinochloa frumentacea (Roxb.) Link. (Japanese millet) from the Far East, and Digitaria sanguinalis (L.) Scop. (manna) from Kashir. Manna was also widely collected as a wild cereal in southern Europe until historical times. It is known to be an important cultivated cereal only in Kashmir and the Caucasus. Proso millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) are the only known Asiatic cereals that were grown in Europe during prehistoric times. The oldest known cereal agriculture in India was practiced by the Harrapans from the Punjab and the Indus Valley. They were growing wheat, barley, and sorghum by 4500 B.P. (Vishnu-Mittre, 1977). These are introduced cereals, wheat and barley from the Near East and sorghum from Africa. Indigenous rice was added to this complex during the late fifth millennium B.P., and other native cereals were locally domesticated during the Indian Bronze age (3700–3000 B.P.) or later. It is also during the Bronze age that African Eleusine coracana (L.) Gaertn. (finger millet) was introduced to South India. The oldest known Asiatic cereals are rice (Oryza sativa), proso millet (Panicum miliaceum), and foxtail millet (Setaria italica). The two millets are ancient cereals from across Eurasia. They were grown in Central Europe some five millennia ago (Heer, 1886) and were widespread in Yang-shao sites from southern Shensi and Shansi provinces in China dating back at least six millennia (Ho, 1977). Wild foxtail millet occurs across temperate Eurasia and could have been independently domesticated in Europe and China (deWet et al., 1979). Wild Panicum miliaceum is known only from Central Asia (Kitagawa, 1937, 1979), and proso millet seems to be truly a Chinese domesticate. If this is true, the presence of proso millet in Europe by 5000 B.P., and possibly in Greece by 8000 B.P. (Hopf, 1962), is surprising. In Europe this millet is commonly associated with wheat and barley. These Near Eastern cereals, however, did not reach China until 3500 B.P. (Ho, 1969). It seems possible that wild Panicum miliaceum is or was at one time more widely distributed than is presently known, and as is true of foxtail millet, was taken into cultivation independently in Europe and Asia. Rice first occurs in the archaeological record of China around 5700 B.P., but outside the assumed Neolithic nuclear area of plant domestication (Ho, 1977). It appears as a cereal in India more than a millennium later. Rice is known from around 4300 B.P. in Harappan sites from Rangpur and is widespread along the lower Indus Valley and southern India about 1,000 years later (Vishnu-Mittre, 1977). Solheim (1971) reports that rice impressions, dating back to around 5000 B.P., are present on pottery from Non Nok Tha in Thailand. It is not possible to determine whether these impressions are of wild or cultivated rice. Wild Oryza sativa is native across South Asia (Oka, 1974). The practice of cereal cultivation was probably introduced to northwestern India from the Near East, and from here or perhaps Africa to southern India some 5,000 years ago. Gorman (1977) proposes that rice was domesticated, together with several rootcrops, in southeastern Asia, and suggests that the initial domestication dates back some nine millennia. Chin (1971), however, concludes that rice farming dates from around 5500 B.P. at Non Nok Tha and Ban Chiang in Thailand, essentially the same date that is suggested by Ho (1977) for rice

cultivation in China. Chang (1976) suggests that rice was first cultivated in ancient India, and that the wide dispersal of this cultigen from this nuclear area led to the formation of three ecogeographic races, indica, sinica, and javanica. It seems equally likely, however, that rice was independently taken into cultivation in at least these three general regions, and that this noncentric (Harlan, 1971) domestication of rice allowed for the development of ecogeographic complexes.

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Rice is the principal cereal in South Asia. The other Asiatic cereals are important in more localized regions. Proso millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) are extensively grown in Central Asia and India. Jobs tears (*Coix lacryma-jobi*) is cultivated in Assam and adjacent Burma, and the Philippines (Arora, 1977). Domesticated races of *Coix* from these two regions are distinctly different, and this crop may have been independently domesticated in northeastern India and the Philippines. Raishan (*Digitaria cruciata*) seems to be an endemic, and possible recent crop of the Khasi hills in Assam (Singh & Arora, 1972). Japanese millet (*Echinochloa frumentacea*) and the Indian shama (*E. colona*) may represent complexes of the same cereal species (Yabuno, 1966). Khodo millet (*Paspalum scrobiculatum*) has been widely grown across the Indian plains at least since the beginning of the Indian Bronze age (Kajale, 1977). *Setaria glauca* (korali) is a Kharif crop in central India, and *Brahiaria ramosa* (anda korra) is little more than an encouraged weed in South India.

As in the Near East, pulses played an important part in the history of agriculture in South Asia and the Far East. The soybean, *Glycine max* (L.) Merr., is an early domesticate from China (Hymowitz & Newell, 1977). Chickpea, *Cicer arientum* L., black gram, *Vigna mungo* (L.) Hepper, pigeon pea, *Cajanus cajan* (L.) Hutch., are native crops of South Asia (Ladizinsky & Adler, 1976; Dana, 1976). The winged-bean, *Psophocarpus tetragonolobus* (L.) DC., is extensively grown in the tropics of Southeast Asia (Hymowitz & Boyd, 1977), and the mung bean, *Vigna radiata* (L.) Wikz., is important across the Orient for its nutritious seeds, edible pods, and young sprouts.

AFRICAN COMPLEX

Cereals grown during prehistoric times in Africa north of the Sahara are typically Near Eastern in origin. Wheat and barley reached the lower Nile Valley by the middle of the seventh millennium B.P. (Wendorf & Schild, 1976) and were staple food crops of ancient Egypt (Wönig, 1886). This is not surprising. North Africa has a Mediterranean climate, and the Nile Valley floods during summer when crops from the African savanna can be grown (deWet & Huckabay, 1967). Near Eastern cereals reached the highlands of Ethiopia, probably not later than the beginning of the Christian era. But, here they were grown together with native African cereals. The West African savanna and East African highlands produced a cereal agriculture independent from that of the Near East. Native African domesticated cereals include Pennisetum americanum (pearl millet) from the Sahel, Eleusine coracana (finger millet) and Eragrostis tef (Zucc.) Trotter (tef) from the highlands of Ethiopia, and Brachiaria deflexa (animal fonio), Digitaria exilis (fonio), D. iburua Stapf (black fonio), Oryza glaberrima Steud. (African rice), and Sorghum bicolor (sorghum) from the savanna of western Africa.

The antiquity of native cereal cultivation in Africa is not known. Archaeological remains of finger millet from Ethiopia are estimated to date back five millennia (Hilu et al., 1979). This archaeological race of Eleusine coracana has lost the ability of natural seed dispersal, and cereal agriculture in Ethiopia must be substantially older. Wild *Eleusine coracana* is distributed across the highlands of East Africa, but this cereal was probably domesticated in Ethiopia (Hilu & deWet, 1976). Finger millet reached South India around 3500 B.P. (Vishnu-Mittre, 1977). Remains of pearl millet dating back to the third millennium B.P. were uncovered at a lake edge settlement in Mauritania (Munson, 1976). A sequence from gathering wild grasses to growing pearl millet is obvious in this settlement. However, it is unlikely that *Pennisetum americanum* was domesticated at the western edge of the Sahel. Wild pearl millet occurs in the central Sahel and highlands of the central Sahara, the region where this cereal was probably first cultivated (Brunken et al., 1977). Pearl millet was introduced to India and became widely cultivated in semiarid parts of South Asia more or less at the same time as its probable spread across the arid savanna of Africa (Vishnu-Mittre, 1969, 1971). The known archaeological record of sorghum, the most important native cereal, dates back in Africa for only two millennia (Connah, 1967; Clark & Stemler, 1975). But, it was an important crop in India as early as three millennia ago (Vishnu-Mittre, 1974). It is, however, an African rather than Indian cereal domesticate (deWet & Harlan, 1971). Wild Sorghum bicolor extends across the African savanna and is commonly harvested as a cereal (deWet, 1978).

Archaeological evidence of early cultivation of other native African cereals are almost completely lacking. The minor African cereals remain more or less endemic to the regions of their probable first cultivation. Wild Eragrostis pilosa (L.) P. Beauv., the probable wild ancestor of tef, is widely distributed and extensively harvested in East Africa (Barth, 1821–1865), but tef is grown as a cereal only on the Ethiopian highlands. Animal fonio is an endemic crop of the Fouta-Djalon in Guinea, while true fonio, black fonio, and African rice are grown as cereals only in the West African savanna (deWet, 1977). African rice is primarily a crop of the Niger delta. It never became a major crop in the wet forest east of the Bandama river. Here the principal food is indigenous yams (Baker, 1962). The paleontological record shows that the Sahara was substantially wetter some 8,000 years ago than it is now, and it is known that around 7000 B.P. people with cattle, sheep and goats were camping along edges of shallow lakes and were probably harvesting wild cereals in areas that are now desert (Clark, 1976). During the next several millennia the Sahara became progressively drier, and by 4000 B.P. the desert extended across most of North Africa. It was probably these

nomadic herdsmen, who migrated south into the present savanna, that eventually domesticated the wild cereals they used to harvest. Pearl millet and sorghum are the principal and possibly oldest domesticated cereals of the African savanna. They, together with cultivated indigenous yams and the pulses, *Voandzeia sub-terranea* (L.) Thauars. (bambara groundnut) and *Vigna ungulata* (L.) Walp (cow pea), made a settled way of life possible. These early farmers made possible cultures that eventually produced the magnificant terracotta and bronzes of Benin around the beginning of the Christian era (Shaw, 1976). Sorghum, pennisetum, cow pea, and the bambara groundnut spread east and south along the savanna,

and they together with finger millet and *Dolichos lablab* L. (an East African pulse) fed the iron age cultures that flourished across southern Africa until the eighteenth century (Fagan, 1967; Robinson, 1966; Summers, 1958).

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NEW WORLD COMPLEX

Five cereal species were domesticated in the New World. Brittle grass, Setaria geniculata (Lam.) Beauv., was extensively harvested in northwestern Mexico and on the Mexican Central Plateau during prehistoric times (Callen, 1965). This species constituted an important part of the diet of the inhabitants of El Riego cave in Tamaulipas some 7,000 years ago. What is of interest, is that the grains of this cereal steadily increased in size during the 2,000 years it was used as a food, suggesting to Callen (1967) that it must have been cultivated. It was eventually abandoned as a cereal after the introduction of maize to the region and is not known to have been grown during historical times. Sauwi (*Panicum sonorum* Beal) is an endemic cultivated cereal of the Warihio Indians in southwestern Chihuahua (Gentry, 1942). It is grown among maize, harvested, and the grains are ground into flour and either mixed with milk to produce a drink, or mixed with maize flour to make pinole. Wild Panicum sonorum extends from southern Arizona to Honduras. The cultivated race retains the ability of natural seed dispersal. Escaped cultivated kinds, recognized by grains that are larger than those of wild races, are widespread around Alamos in Sonora, and around archaeological ruins in Nyarit and Jalisco, suggesting that sauwi may have been more widely cultivated before the introduction of corn to northeastern Mexico. It is surprising that Father Kino (1684–1685), a missionary and early explorer of northwestern Mexico did not mention this native millet in his writings. Today the species is valued more as a fodder for livestock than as a cereal grain. Mango (Bromus mango) is the only known domesticated cereal that is not an annual. Claudio Gay (1865) was one of a few South American botanists who actually saw this cereal in relatively extensive cultivation. Gay writes that before the conquest, the people of central Chile made a kind of bread without yeast that they called covque, and that this bread was made from a native cereal known as mango. He visited central Chile in 1837 and found mango growing in two fields in the department of Castro. The species is biannual. At the time of his visit to this part of Chile, livestock were allowed to graze on the fields during the first season of growth. Plants were protected from livestock the next year and produced a cereal crop in the fall. Mango was harvested, threshed, and the grain was ground into flour that was used to make bread or chicha. Bread and chicha made from mango were reported to be inferior to that made from the wheat and apples that were extensively grown around Castro by the early nineteenth century. Gay (1865) mentions a possible second cereal that used to be grown in Chile. It resembled barley, except that the grains were smaller, and it was harvested while the plants were green to prevent the inflorescence from shattering. Laet (1633) describes a cereal called teca, similar to barley, with stems like oats and grains a little smaller than those of rye. Whether teca is the second cereal described by Gay is impossible to ascertain with certainty (Parodi & Hernández,

1964). Later, Molina (1782) talks about two native cereals in Chile, "el Magu," a species of rye, and "la Tuca," a kind of barley. He unfortunately saw neither of these cereals in cultivation. They were already replaced by wheat and barley when his natural history of Chile was written. Ball (1884) reports that the Araucano Indians of Bahia Blanca in Argentina use *Bromus unioloides* H.B.K. (*B. catharticus* Vahl) as a wild cereal. It is possible that this wild cereal represents the teca of Laet (1633) and tuca of Molina (1782).

The only New World cereal of present day importance is Zea mays (maize). It was domesticated in Mesoamerica, became widely distributed across the New World by the time of conquest by Europeans, and has since been dispersed across all tropical and warm temperate farming regions of the Old World. Wherever it is adapted, maize is replacing native African and Asiatic cereals except for rice. Maize is unique in female inflorescence morphology among grasses. The paired female spikelets are arranged in more or less indurated cupules along and around a central rachis in usually eight or more rows. The closest wild relative of maize, Z. mays subsp. mexicana (teosinte) has a distichous female inflorescence. The oldest indisputable maize known in the archaeological record comes from the Coxcatlán culture phase of the Tehuacán Valley in Mexico (Mangelsdorf, MacNeish & Galinat, 1967a). This maize dates back some 7,000 years and is assumed to be wild maize by Mangelsdorf and his coworkers (Mangelsdorf, 1974). Beadle (1977) points out, however, that this maize lacks the ability of natural seed dispersal and must have been cultivated.

The antiquity of cereal agriculture in the New World is not known. MacNeish (1971) suggests that Barranca horticulture started in Tehuacán Valley between 7000 and 5000 B.C., and Niederberger (1979) points out that fully sedentary communities existed in the Basin of Mexico at least since the sixth millennium B.C. Be that as it may, maize was grown on the Mexican plateau some 7,000 years ago, and if teosinte is wild maize, which is almost certain, it must have been taken into cultivation considerably earlier than during the Coxcatlán culture phase of Tehuacán. Teosinte does not occur in the arid Tehuacán Valley, but is distributed along the western escarpment of the mountains and the wetter parts of the Mexican plateau (Wilkes, 1977).

From its center of domestication in Mesoamerica maize spread rapidly across the Americas. It is known to have been cultivated in New Mexico and Arizona not later than 4000 B.P. (Mangelsdorf, Dick & Cámara-Hernández, 1967), and also reached northwestern Mexico as a cereal some 4,000 years ago (Mangelsdorf, MacNeish & Galinat, 1967b). Maize was grown in Ecuador during the early formative stage dating back some 5,000 years (Zevallos et al., 1977).

In the Americas maize evolved with beans (*Phaseolus vulgaris* L. and *P. lunatus* L.), squash (*Cucurbita* spp.), and amaranths as staple foods (Kaplan, 1965; Gentry, 1969; Baudet, 1977). Only in the wet tropics and high Andes are tubers more important than maize. Indeed, maize is such an excellent cereal, with such good nutritious qualities and a wide range of adaptations, that its domestication probably excluded several other potential cereals from being taken into cultivation. It is known that maize replaced *Setaria geniculata* in Mexico and *Bromus mango* in Chile as planted cereals.

Indian wild rice (*Zizania aquatica*) is a newly domesticated cereal. The species is widely distributed in temperate North America from the Dakotas east to the Atlantic coast and south to Florida and Texas. In the northeast, and in Wisconsin, Minnesota, and adjacent Canada wild rice is extensively harvested. Hofstrand (1970) estimates that some 40,000 acres of natural stands are commercially harvested in Minnesota and Wisconsin alone.

The range of wild rice has probably been extended by sowing ever since it was first used as a cereal. It is easy to establish along shores of shallow lakes. Attempts to grow Zizania successfully, however, have until recently failed. The first serious attempts to grow wild rice commercially in paddies date back less than two decades (Oelke et al., 1973). Since 1971 production of wild rice in manmade habitats exceeds that harvested from natural stands in Minnesota (Brunson, 1972). Success in growing Zizania followed the discovery of a population with poor seed dispersal ability. It is estimated that in wild stands some 90% of grain escapes the harvester due to natural seed dispersal. Less than 50% of the grain is naturally dispersed in improved races grown commercially (deWet & Oelke, 1978).

ORIGINS AND CONSEQUENCES OF FOOD PRODUCTION

The shift from hunting and food gathering to animal and plant husbandry ranks with the industrial revolution as one of the great achievements of man. Huntinggathering is not necessarily a difficult way of life. Gathering wild food is less labor demanding than growing the same plants for food (Bronson, 1977). Bushmen and other present-day nomadic hunter-gatherers devote at most a few hours a day to subsistance activities (Lee, 1972). However, a nomadic way of life limits cultural evolution. Settled communities demand a regular food supply in the area of settlement. This is best achieved through agriculture. Why the shift from hunter-gatherer to settled agriculturist occurred during the culture history of man is not known. Man must have had a basic knowledge of plant cultivation long before he actually started to domesticate plants by consciously sowing what was harvested from a planted population. The Indians of the Great Basin of western North America were specialized harvesters of wild cereals, who sowed to increase the population density of the fields to be harvested. Similarly, gardens of wild food plants are often maintained around temporary settlements of nomadic herdsmen. Sowing experiments are continued for a few generations and then abandoned.

Plant and animal husbandry evolved over several millennia, and settled farming is a relatively recent innovation of man that does not date back much beyond 10,000 years. The possible reasons why farming did not evolve earlier during the culture history of man are discussed by Bronson (1977). He suggests four possible explanations for this delay in food production. The first is labor saving. As already pointed out, gathering plant food and hunting are less labor intensive than farming. Second, time was required for reliable cultivated crops to evolve. Food crops probably were grown for millennia before evidence of domestication became obvious in the archaeological record. Third, farming de-

veloped as an adaptive response to increase in population numbers. Plant husbandry was not necessary when populations were small (Cohen, 1977). Fourth, farming involves risk. The hunter-gatherer had to invest a substantial amount of labor and resources in growing food crops without a guarantee of success. Crop failure is still common and often leads to famine.

Smith (1972) suggests that food production was initiated on a number of occasions by different groups of hunter-gatherers when faced with a gradual reduction in productivity of effort required to maintain the "culturally approved standard of living and the traditional group size and social organization." Once initiated, population pressures in particular will tend to demand and intensify agricultural activities. A combination of these and other factors probably led to the beginnings of agriculture. From a botanical point of view, certain species lend themselves to domestication while others are almost impossible to domesticate (deWet & Harlan, 1975; deWet, 1979). American wild rice, Zizania aquatica, does not readily adapt to man-made habitats. Although it was extensively sown in natural habitats, it was not domesticated by Amerinds (Dore, 1969; deWet & Oelke, 1978). Only natural colonizers are readily cultivated as annual seed crops. Planting of seeds harvested from previously man-sown populations may have first become important to preserve selected traits. It seems likely that teosinte was taken into cultivation to preserve a newly discovered tunicate allele. The oldest known maize from Tehuacán is distinctly tunicate. It has soft, papery glumes. This mutation not only induces some stability to the rachis of teosinte, and thus facilitates harvesting, but also greatly enhances threshing the grain from the otherwise indurated glumes. The common characteristic of domesticated cereals, their inability of natural seed dispersal, may also have been a trait that was consciously selected by man. Harvesting by sickle (Wilke et al., 1972) in association with sowing (Harlan et al., 1973), however, automatically leads to a gradual loss of mechanisms for efficient natural seed dispersal. Be that as it may, wherever grasses were extensively harvested and agriculture was possible, selected species that were preadapted to withstand habitat disturbances by man eventually became domesticated. Cereal agriculture seems to be oldest in Southwest Asia. Carter (1977) argues that the idea of plant and animal husbandry spread slowly from this nuclear center across the Old World and eventually to the Americas. Conclusive evidence for a diffusion of the knowledge of agriculture between the Old and New Worlds is lacking, however, and it seems more likely that agriculture evolved independently in several regions of the Old and New Worlds. Different species were domesticated at different times in the Near East, Far East, African savanna, and New World without evidence of exchange of crops among centers during the earlier stages of domestication. Civilizations developed independently in the Old and New Worlds until late historical times. Accidental contacts may have occurred between Europe and the east coast of North America, and between the west coast of both Mesoamerica and South America and Asia (Carter, 1977; Lathrap, 1977). However, even if true, cultural exchange must have been minimal. It was not until the fifteenth century that Old World crops were brought to the New

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World in exchange for such important New World crops as maize, potato, sweet potato, garden beans, tomato, and peppers.

Cultural contact between the Near East and Europe is obvious in the archaeological record at least since 8000 B.P. Near Eastern agriculture also spread to ancient Egypt where wheat and barley became the basis on which dynastic Egypt was built. Near Eastern influences probably reached the African savanna civilizations around the seventh century A.D. with the expansion of Islam across North Africa (Lewicke, 1974). Sorghum races that evolved in India after some 3,000 years of isolation were reintroduced to Africa during this time (Harlan & Stemler, 1976). Contact of the Near East with the Far East occurred around 1500 B.C. when wheat and barley reached China (Ho, 1969). Food production has advantages over food gathering. However, several societies never adopted agriculture. The aborigines of Australia, the bushmen of southern Africa and several jungle tribes in Africa, Asia and the Americas, even today shun a settled way of life. Comparing these hunter-gatherer societies with farmers, it is obvious that food production has substantially accelerated the social evolution of man during the 400 or so generations since the beginnings of cereal cultivation (Childe, 1936). What are the consequences of food production? Rousseau (1755) argues that agriculture made organized work a necessity, forests were destroyed to make way for crops, individual ownership of property was introduced, and slavery developed. Survival of "civilized" man became dependent on cereal agriculture. Overpopulation, depletion of the world's resources, planetary pollution, and the social ills of cities are penalties we have to pay for the pleasure of an abundant and stable food supply. The social consequences of village life are discussed by Smith (1972), and fall outside the scope of this manuscript. More important from the point of view of a botanist is the impact of farming on the immediate environment. Food production permits a greatly increased population density per unit area over that characteristic for hunter-gatherers. Cipolla (1964) estimates that the world's population was between five and ten million some 10,000 years ago when man first practiced conscious plant and animal husbandry. Hunter-gatherers live in equilibrium with the environment and have little lasting effects on nature. Farming by its very nature destroys the natural environment. Habitats are permanently altered, and a return to hunting and food gathering becomes impossible. Food production, for better or for worse, is here to stay. We must learn to cope with the pleasures as well as ills of civilization.

Weeds and domesticates evolved in the permanently disturbed man-made habitat. Domesticates are cared for, and we depend on them for our food supplies. They are carefully selected for total fitness in specific environments, and their population sizes are carefully controlled by man. Weeds are spontaneous in the man-disturbed habitat. Great effort is required to maintain their population growth, lest they totally colonize the habitat in which man grows his crops. Man, the ultimate weed, must learn to control his own population growth. Food production can keep pace with the human population explosion for the immediate future. However, planetary pollution, shortages of natural resources, and the

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numerous social ills that accompany overpopulation are problems that will intensify. Only when these problems are solved can man hope to again live in harmony with his environment.

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